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Secondary Production of Microcopepods in the Southern, Eutrophic Basin of Kaneohe Bay, Oahu, Hawaiian Islands[1]

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ABSTRACT: The microcopepods function as an important herbivorous group in the planktonic community of the southern, sewage-rich portion of Kaneohe Bay, Oahu, Hawaiian Islands. Most of the microcopepod biomass was composed of a rapidly producing species of Paracalanidae. The Paracalanidae population production rate was calculated with the field population stage composition, the length:dry weight relationship, and the species development rate in both laboratory and *in situ* containers. The population production rate:biomass ratio equalled 78 percent per day during summer 1968. For all of the microcopepods, secondary production was estimated to be 1.8 mg nitrogen/m^3/day.

Kaneohe Bay on the northeast coast of Oahu, Hawaii, contains an isolated, neritic ecosystem. The planktonic component of the community in the southern portion of Kaneohe Bay has become relatively eutrophic (Clutter 1973) in association with the addition of large quantities of nutrients from urban sewage and with stream runoff from surrounding developed lands during heavy, seasonal rains (Hanson 1974). The general consequences of the nutrient level changes for the planktonic community have been numerically modelled (Caperon 1975). The biomass of the microzooplankton, a major portion of which are microcopepods, has increased greatly with eutrophication (Hirota and Szyper 1976). Because small organisms generally have high production rate:biomass ratios, the microcopepods were expected to be quite important in the community's nutrient cycle. The microcopepods have only been the subject of a grazing study in the laboratory that dealt with the late copepodid stages (Szyper 1972). Because the production rate of the field populations was not well understood, we initiated the present study to determine the biomass and secondary production of the microcopepods in southern Kaneohe Bay.

Three species of microcopepods occurred commonly in southern Kaneohe Bay. To indicate the niches of these three species, we will describe very briefly their morphology and feeding. The smallest species was *Oithona simplex*, which has been described at each stage of development by Bjornberg (1972). The *Oithona* feeding appendages are characteristically adapted for seizing and masticating particles, such as the diatom *Skeletonema* and small dinoflagellates about 15 μm in diameter, that are relatively large compared to the body (Gauld 1966, Parsons et al. 1969).

Another species was the cosmopolitan, neritic *Oithona nana*. The development stages of *O. nana* have been described by Haq (1965). The species has fed and been cultured on such organic debris as bits of decaying kelp (Murphy 1923). *Oithona nana* is similar to *O. similis* (Sazhina 1971), which is usually abundant in sewage-rich Norwegian fjords (Wiborg 1944).

The largest of the three microcopepods has been identified as a species of the genus *Paracalanus*. It is probably a species of *Acrocalanus* (Hirota, personal communication), which is another closely allied genus in the family Paracalanidae (Scott 1909, Tanaka 1956). The name of the family, Paracalanidae, has been used in this paper to identify the microcopepod species,

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because the name includes both taxonomic possibilities. There have been two studies of the food of the Paracalanidae in Kaneohe Bay. Szyper (1972) found that the late copepodids fed mainly on cells of small diameter (15 μm), like the diatoms *Skeletonema* and *Chaetoceros*; Hirota and Szyper (1976) have shown by fluorescence analyses of the gut contents that the adult females in nature are mainly herbivorous, although they may be slightly omnivorous.

In the present study, the measurements of population production were made directly on Paracalanidae only, since this species was found to constitute a majority of the microcopepod biomass in southern Kaneohe Bay.

MATERIALS AND METHODS

The microcopepods were collected in the middle of southern Kaneohe Bay at station 9 (21°26′ N, 157°47′ W) of the study that has been described by Clutter (1973). The location of the station also corresponds to station 1X in figure 1 of the paper by Caperon, Harvey, and Steinhilper (1976). To determine the seasonal patterns of abundance, we analyzed 24 samples over a whole year at intervals of usually 2 weeks from August 1968 to July 1969. The sampling was done between the hours of 0900 and 1200. The samples were collected from the upper 11 m of a water column that was usually 14 m deep.

The plankton sampler, which was lifted vertically, was specially designed for a 1968–1969 study (Clutter 1973: 192). The sampler was similar to a Bongo net, having two, bridleless nets attached to a frame that positioned the nets vertically on the sides of the towing cable. One of the nets, the microzooplankton net with which the microcopepods were obtained, was made of 64 μm Nitex with an inner liner of 333 μm Nitex; this allowed only the 64–333 μm size fraction to be sampled. The microzooplankton net had a conical, nonfiltering collar that reduced the mouth diameter to 35 cm. Preliminary field tests showed that the collar and the 64-μm mesh allowed a filteration efficiency of nearly 100 percent.

The density of the microcopepod species and stages was determined with subsamples of the samples. The subsamples were obtained with a Hensen-Stempel pipette after the sample had been diluted to 300 ml and had been thoroughly agitated. Subsamples were removed until 12 subsamples or 40 animals per developmental stage had been counted.

The range of statistical variability due to patchiness and subsampling was calculated with four subsamples from each of six replicate samples. The replicate samples were collected during one-half hour on 4 August 1972 in the above-described manner at the same station location. The range of the 95-percent confidence limits for the logarithm-transformed data (Winsor and Clarke 1940) equalled very nearly $\frac{2}{3}$ to $\frac{3}{2}$ of the abundance in a single sample for each of the three microcopepod species. The range of the 95-percent confidence limits of a single sample usually exceeds $\frac{1}{2}$ to $\frac{2}{1}$, as a result of natural patchiness alone (Wiebe and Holland 1968).

A method was needed that would allow us to estimate the relative rates of population production per unit biomass for the three species. We estimated the relationship of the three ratios by calculating the maximum rates of increase in abundance of each species during their seasonal fluctuations in abundance. The rates of increase were calculated with the observed increases in only copepodid abundance, because data were not available for all three species either on the entire population abundances or on biomasses. The following equation was used for the calculations:

$$N_t = N_o e^{rt}, \quad (1)$$

where r is the exponential rate of increase and t is the time span between the initial and final counts of abundance, N_o and N_t, respectively. The rates of increase in units of population biomass instead of copepodid abundance probably would be similar, because the copepodids constituted about 80 percent of the total population biomass, and further, because the stage compositions probably did not vary greatly throughout the season, as indicated by the percentage of adults in each population (Bartholomew 1973: figures 5, 6, and 7). Because sampling variability would have influenced the separate measures of abundance, the rates were calculated and averaged for the five periods of most rapid increase of each species. Measurements from periods of rapid increase were used

because the rates of population recruitment and production during those periods are generally large in comparison with the rates of yield or loss; therefore, the rates of rapid increase in abundance are probably a good indication of the species' gross rates of population production per unit biomass.

The Paracalanidae production rate in southern Kaneohe Bay was calculated by a method that required the stage specific abundance, weight, and development rate. We determined the stage specific abundance, or population stage composition, of the natural population with a series of samples for a period (August 1968) of relatively stable Paracalanidae abundance. The use of several samples gave a precise estimate of the average population composition during this period. Since the naupliar stages were sampled inadequately by the 64-μm net under water pressure from towing, the average abundance per stage of the nauplii was estimated with the following equation:

$$N_{(i+1)} = N_i\, e^{-dt}, \qquad (2)$$

where N_i and $N_{(i+1)}$ are the abundances of the i^{th} and $(i^{\text{th}}+1)$ stages, t equals the development time between successive stages, and d is the instantaneous mortality rate. The instantaneous mortality rate was calculated for the interval from copepodid stage I to II with the observed decrease in abundance and the measured development time, and then the abundance was estimated for each naupliar stage with the above equation. The estimations assume that the instantaneous mortality rate of the early copepodids was characteristic of the nauplii. During a similar study of a microcopepod in an estuary, Heinle (1966) found that the average mortality rates for the naupliar and copepodid stages differed by only 30 percent.

The total body length of the Paracalanidae copepodids and adults was related to the dry weight of the specimens. (The total body length measurements excluded the caudal setae.) Fresh specimens were caught during August 1972, then chilled to allow easier sorting and measurement, rinsed briefly in distilled water, and dried overnight at 60° C. The dry weight was measured with 7–15 animals per sample to the nearest 0.5 μg with a Cahn electrobalance. We measured the carbon and nitrogen contents in an F & M model 185 CHN analyzer, using 18 to 48 animals per sample. The dry weight of both *Oithona* species was measured with only the adult females; the relative biomass of the whole populations, including the other developmental stages, was assumed to approximate the measured ratio of adult female dry weights.

The development rate of Paracalanidae was measured in two different situations. First, the development rate was measured in the laboratory in 1-liter flasks half-filled with bay water. An abundant food supply was maintained in the containers by constant illumination and agitation on a shaker table. The temperature in the containers was maintained at 30° C, which was similar to the high, summer, surface temperature of the bay, but which was warmer than the bay during the time of this experiment (21 to 28 April 1972). The development rate of Paracalanidae was measured also *in situ* in the small and very eutrophic lagoon that is adjacent to the Hawaii Institute of Marine Biology in southern Kaneohe Bay. The *in situ* method was similar to the method of Heinle (1966): clear plastic cylinders of 2.2 liters were covered on the ends with 40-μm mesh so that metabolites and food could circulate. During the experiment, from 30 July to 7 August 1972, the lagoon surface temperature where the containers were suspended varied from 27° to 29° C. The containers for both the *in situ* and laboratory development rate experiments were inoculated with water that had been filtered through 64-μm Nitex mesh. Examination of the inoculum showed that only the Paracalanidae stage I nauplii and presumably eggs had passed through the 64-μm mesh into the containers. After the 16 containers had been inoculated, the stage composition in two of the containers was examined every day for calculation of the species' development rate.

The daily Paracalanidae population production rate was calculated by a method similar to that used by Mann (1969) with the following equation:

$$P_{i\to(i+1)} = \frac{N_i + N_{(i+1)}}{2}\,[W_{(i+1)} - W_i]\,\frac{1}{t} \qquad (3)$$

where $P_{i\to(i+1)}$ equals the daily production in dry weight per m^3 of the Paracalanidae during the i^{th} to the $(i^{\text{th}}+1)$ stage interval; N and W are the density per m^3 and dry body weight,

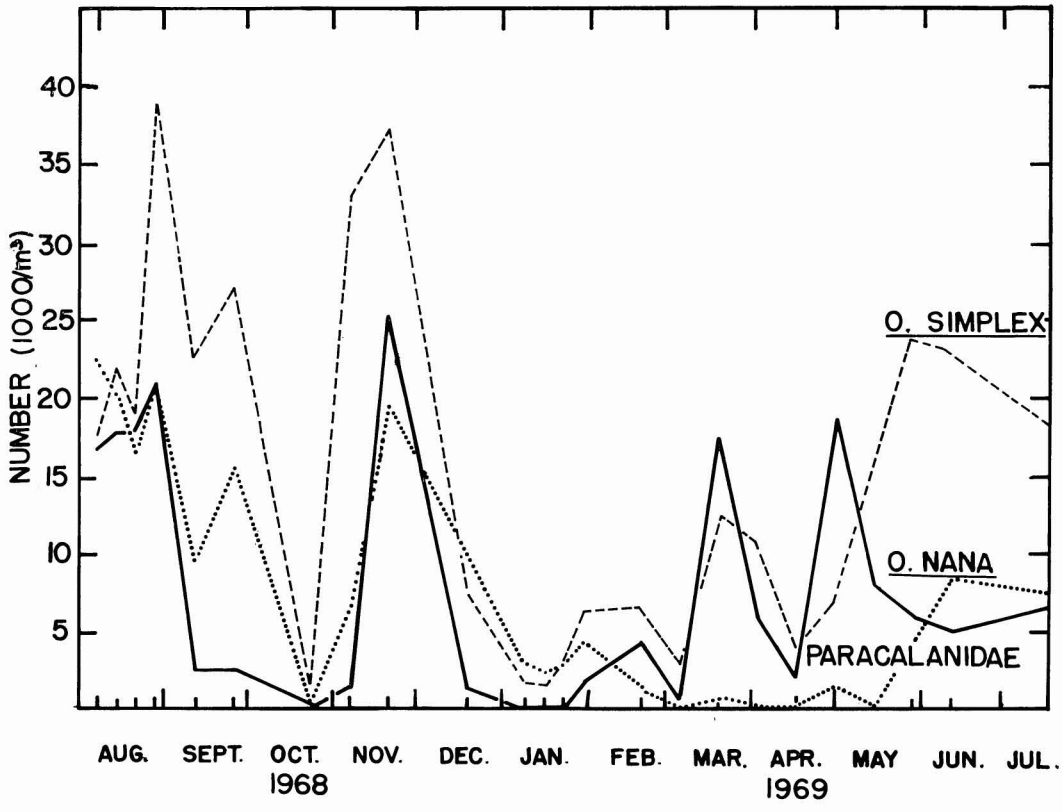

FIGURE 1. The seasonal abundance of three microcopepod species in southern Kaneohe Bay during 1968–1969. The abundances are for copepodids in the 64–333 μm size fraction.

respectively, of animals in the i^{th} or $(i^{\text{th}}+1)$ developmental stages; and where t equals the development time between the i^{th} and $(i^{\text{th}}+1)$ stages. In order to account for the exponential rates of change in abundance between the developmental stages, we calculated the average density $\left[\frac{N_i+N_{(i+1)}}{2}\right]$ with logarithms.

RESULTS

In southern Kaneohe Bay, the Paracalanidae, *Oithona simplex*, and *O. nana* populations were found to comprise 99 percent of the total copepod abundance in the 64 to 333 μm size fractions. The abundances are shown in Figure 1 of the copepodids (including adults) of the three species in southern Kaneohe Bay during the 1968–69 sampling period. All three species were characterized by large seasonal fluctuations in abundance. During the spring, the Paracalanidae population increased first and was followed by increases in the *O. simplex* and then *O. nana* populations.

The exponential rates of increase of the copepodids (Table 1) have been measured and averaged for the five periods of most rapid population increase of each species. The average rate and maximum observed rate were highest for the Paracalanidae population. The rates for *O. nana* and *O. simplex* were similar, their average rates both being 38 percent lower than the average for Paracalanidae.

The relative population size of the three species was calculated for two periods of time. During both the whole 1968–1969 sampling period and during the August 1968 period of relatively stable abundances, the average density of *O. simplex* was about twice the density of

TABLE 1

The Exponential Rates of Increase of Copepodids for Three Microcopepod Species in Southern Kaneohe Bay during Five Periods in 1968–1969

Species	Period	Initial and final copepodid abundances (no. per m^3)	Exponential rates of increase in abundance (day^{-1})
Paracalanidae	23–29 Jan	150–1,752	.41
	5–19 Mar	696–17,628	.23
	16–30 Apr	2,052–18,576	.16
	23 Oct–6 Nov	198–1,506	.14
	6–20 Nov	1,506–25,638	.20
Oithona nana	23–29 Jan	3,048–4,500	.06
	5–19 Mar	102–798	.15
	14–28 May	246–4,050	.20
	28 May–12 Jun	4,050–8,250	.05
	23 Oct–6 Nov	348–6,852	.21
Oithona simplex	15–23 Jan	1,698–3,102	.08
	23–29 Jan	3,102–6,216	.12
	5–19 Mar	2,898–12,480	.10
	21–28 Aug	18,900–39,600	.11
	23 Oct–6 Nov	1,452–33,000	.22

TABLE 2

The Relative Population Size of Three Microcopepod Species in Southern Kaneohe Bay

Species	Copepodid abundance (no./m^3)	Adult female dry wt. (μg/animal)	Relative population biomass (%)
Paracalanidae	20,022	2.79	64
Oithona nana	21,558	.74	18
Oithona simplex	37,112	.41	18

Note: The abundances are averages for copepodids only in 64–333 μm size fraction in the four samples from August 1968. The estimated population biomasses are percentages of the estimated total biomass of microcopepods.

Paracalanidae and *O. nana*. The relative biomasses of the three species were estimated by multiplication of the abundances by the body weights (Table 2). The calculations show that during August 1968 or during the whole 1968–1969 sampling period when the relative abundances were similar, the estimated population biomass of Paracalanidae was higher by a factor of about 3.5 than was the biomass of each *Oithona* species.

The population production rate was calculated for only Paracalanidae for the period of relatively stable abundances during August 1968. For the four August 1968 samples, the density of each copepodid stage is shown in Table 3 as the average number per m^3 in the upper 11 m of the water column. The mean density of each nauplier stage has been enclosed in parentheses to indicate that the numbers were estimated with equation no. 2 as previously described.

The average biomass of the Paracalanidae at each stage of development (Table 3) was calculated with a relationship of total body length to

TABLE 3

CALCULATIONS OF THE POPULATION PRODUCTION RATE OF PARACALANIDAE IN SOUTHERN KANEOHE BAY DURING AUGUST 1968

STAGE	DENSITY (N) (no./m³)	DRY WEIGHT (W) (μg/animal)	BIOMASS ($N \times W$) (mg dry wt/m³)	STAGE DURATION (t) (days)	AVERAGE LOGARITHMIC DENSITY $\frac{N_i + N_{(i+1)}}{2}$ (no./m³)	WEIGHT INCREASE $\Delta W_{(i+1)-i}$ (μg dry wt)	PRODUCTION RATE $P_{i\to(i+1)}$ (mg dry wt/m³/day)
Nauplius							
I	(33,463)	(.004)	.13	–	–	–	–
II	(25,346)	(.006)	.15	.5	22,058	.014	.62
III	(19,198)	(.02)	.38	.5	16,708	.03	1.00
IV	(14,542)	(.05)	.73	.5	12,656	.02	.51
V	(11,015)	(.07)	.77	.5	9,586	.02	.38
VI	(8,343)	(.09)	.75	.5	7,261	.04	.58
Copepodid							
I	6,320	.13	.82	.8	5,060	.14	.88
II	4,052	.27	1.09	.8	3,199	.42	1.68
III	2,526	.69	1.74	.8	2,459	.31	.96
IV	2,394	1.00	2.39	.9	2,243	.82	2.04
V	2,103	1.82	3.83	.9	2,103	.76	1.78
Adult	2,627	2.58	6.78	–	–	–	4.75

NOTE: Numerals in parentheses represent the estimated abundance and dry weight of naupliar stages.

The daily Paracalanidae population production rate was calculated by a method similar to that used by Mann (1969) with the following equation: $P_{i\to(i+1)} = \frac{N_i + N_{(i+1)}}{2} [W_{(i+1)} - W_i] \frac{1}{t}$, where $P_{i\to(i+1)}$ equals the daily production in dry weight per m³ of the Paracalanidae during the i^{th} to the $(i^{th}+1)$ stage interval; N and W are the density per m³ and dry body weight, respectively, of animals in the i^{th} or $(i^{th}+1)$ developmental stages; and where t equals the development time between the i^{th} and $(i^{th}+1)$ stages. In order to account for the exponential rates of change in abundance between the developmental stages, we calculated the average density $\left[\frac{N_i + N_{(i+1)}}{2}\right]$ with logarithms. The adult production rate was estimated with the P:B ratio for the late copepodids.

dry weight. The relationship for fresh Paracalanidae copepodids during August 1972 was as follows:

$$\log_{10}(\mu\text{g dry wt}) = 2.96 \log_{10}(\text{mm total body length}) + .89, \quad (4)$$

with a standard error of the estimate of 0.05 and with a 95-percent confidence limit on the slope of ± 0.11. The relationship was used to estimate the dry weight of the naupliar stages (in parentheses in Table 3) because the tiny Paracalanidae nauplii could be measured for body length but could not be sorted in sufficient quantity for weight determination. The weight was different for the males and females of copepodid stages V and VI; the stages V and VI weights in Table 3 are mean weights that were calculated with the weight and relative abundance of each sex. (Males composed 52 and 20 percent of the copepodid stages V and VI animals, respectively.) For conversion of the biomass to units of carbon or nitrogen, the average ratio of dry weight:carbon weight:nitrogen weight was 12.0:4.1:1.0 for Paracalanidae copepodids during August 1972. The relative proportion of nitrogen increased slightly in the late copepodid stages.

The development time for Paracalanidae from nauplius stage I to adult was about 1 week (Figure 2) at 27° to 30° C in both the laboratory and *in situ* lagoon containers. To obtain the stage-specific development times for the production calculations, we determined the average stage composition in both the *in situ* and labora-

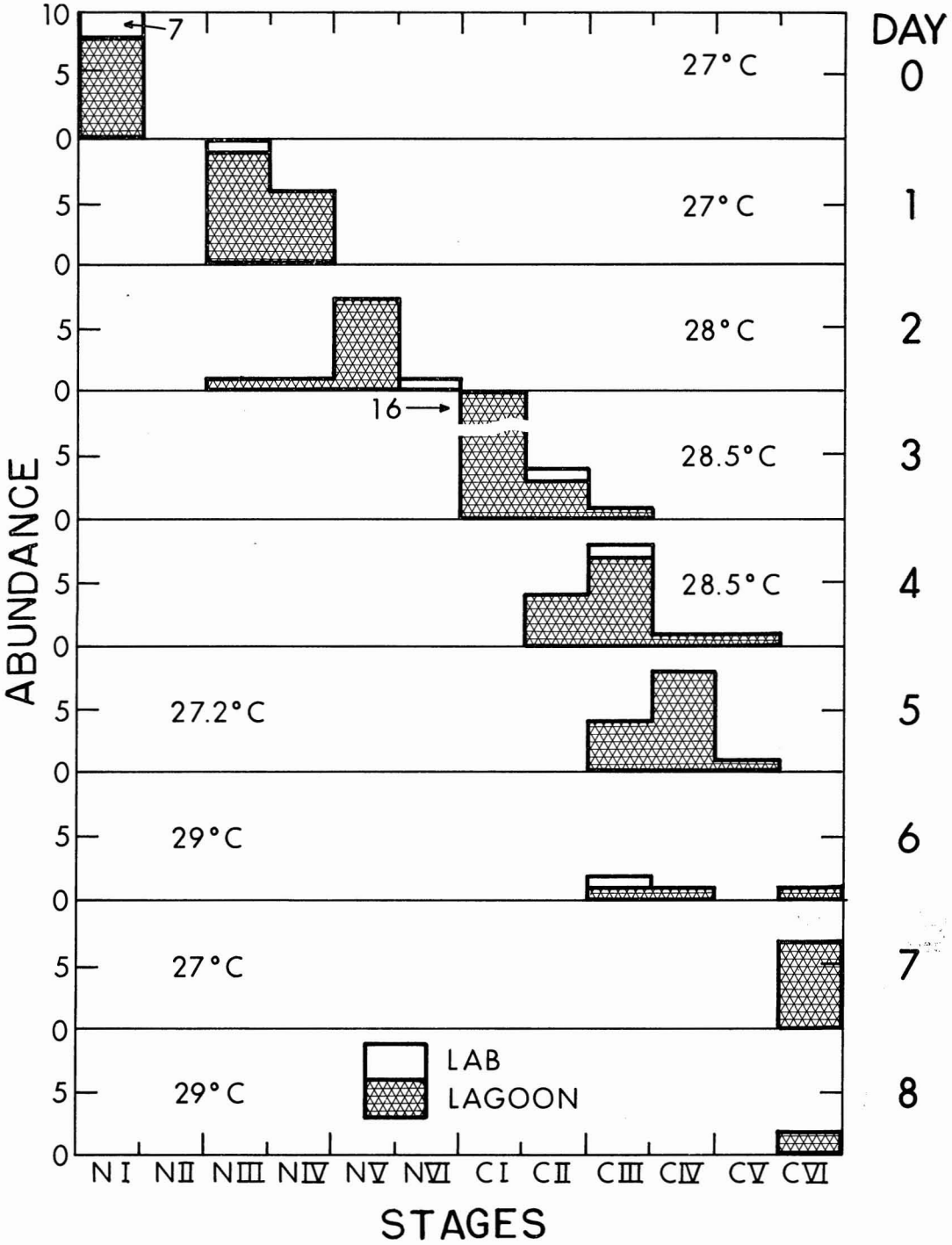

FIGURE 2. The development rate of Paracalanidae in both the laboratory and *in situ* lagoon containers. The temperature that is listed with each histogram is the surface temperature at the time that the sample was preserved for analyses. The temperature of the laboratory experiment was 30° C. The height of the histograms (or the small numbers) indicates the total number of observed developmental stages in both the laboratory and field containers.

tory containers for several time intervals after inoculation. The containers were inoculated on day zero with an unknown ratio of eggs and stage I nauplii. On day 1 the stage distribution had an average of naupliar stage 3.4, and after 2 more days the average was at copepodid stage 1.3. Since the animals' development averaged 3.9 stages in 2 days, a mean stage duration of .5 days per stage was used for the nauplii. The mean stage durations of the early and late copepodids were determined similarly. On days 5 and 7 the average stage distribution was at copepodid stage 3.8 and 6.0, respectively, and after day 7 some of the animals in the containers were probably reproducing and dying. The mean stage duration of the early copepodids, whose development averaged 2.5 stages in 2 days, equalled .8 days per stage; the duration of the late copepodids, whose development averaged 2.2 stages in 2 days, equalled .9 days per stage. The mean duration of the adult stage, during which there is egg production and during which feeding usually continues at a rate similar to the late copepodid stages (Marshall and Orr 1966), was not measured. We calculated the growth rate of the adult stage by multiplying the adult biomass by the growth rate to biomass ratio for the late copepodids.

The data with which the Paracalanidae population production was calculated are in Table 3. With the data, the rate of population production (growth) or yield can be calculated; both rates would be equal when averaged over the whole period of development, as stated by Mann (1969). The rate of production was calculated because the resulting value was less dependent on the estimated weights and abundances of the nauplii. For the calculations, the density during the copepodid V to VI interval was assumed to be equal to the initial copepodid V density of 2103/m^3. Also, the pattern of weight increases during development indicates that the Paracalanidae probably began to feed and grow at only the naupliar II to III interval, so the population production rate was calculated from that interval to the adult stage. Summation of the stage-specific values in Table 3 shows that the population production rate equalled 15.18 mg dry wt/m^3/day, and that the population biomass equalled 19.56 mg dry wt/m^3. The ratio of population production rate to biomass equalled 78 percent per day.

DISCUSSION

The main source of error in the summer production calculation probably lay in the method by which the development time was measured. The development time was probably influenced by the food concentration in the containers in a manner that was similar to the general hyperbolic relationships between feeding rate and food concentration. The 64-μm mesh through which the inoculum was filtered probably excluded some large chains of phytoplankton that might otherwise have served as food for the late copepodid stages. The total concentration of phytoplankton per animal in the containers was probably not limiting because of the high environmental concentration of phytoplankton in the surface water that circulated through the lagoon containers and because of the continuous light provided for phytoplankton growth in the laboratory containers. Further, the development time was measured in containers at 27° to 30° C, which was the lagoon, surface, day temperature, but the temperature was probably higher than the average daily temperature for the entire water column in southern Kaneohe Bay. The laboratory development time of an *Oithona* species was found by Haq (1965) to have a relationship to temperature with a Q_{10} of 3.06. If the development time of Paracalanidae in southern Kaneohe Bay had a similar Q_{10}, the development time and calculated production rate would have been reduced by about one-third with an experimental temperature decrease of only 3.5° C, or with an average summer temperature for the whole water column of 25° C (Bathen 1968). The abundant food concentration and high temperature in the containers, in relation to the average values for the whole water column, gave a summer population growth rate: biomass ratio that was probably high for the Paracalanidae population in southern Kaneohe Bay.

The results of the present study relate to the results of Szyper's (1972) study of the grazing of Paracalanidae copepodids in southern Kaneohe Bay. Szyper (personal communication) calculated a hyperbolic relationship of consumption

rate:food concentration for all of his data, and the conversion ratios for the phytoplankton and copepod weights. The studies by Reeve (1970) and Corner (1972) have shown that the rates of consumption in units of carbon, nitrogen, or dry weight are around 3 to 4 times the rates at which these materials accumulate as growth on the copepodid stages of coastal and neritic copepods. The 3- to 4-magnitude difference indicates that the consumption rate:biomass ratios of Paracalanidae copepodids might theoretically be 3 to 4 times the production rate:biomass ratios of the animals. Yet, the calculated maximum (R_{max} of the hyperbola) consumption rate:biomass ratio of Szyper's data was actually eight times the production rate:biomass ratio for the late copepodids during summer in the present study. The eightfold difference indicates that the 78-percent ratio of Paracalanidae population production rate:biomass may be only about one-half of the maximum ratio for this microcopepod population at higher food concentrations.

The consumption rate:biomass ratio of microcopepods has been examined also in temperate, coastal waters by Parsons et al. (1969) and by Petipa, Pavlova, and Mironov (1970). The former study included an experiment with some *Oithona*, but most of the copepod biomass in the experiment was composed of the species *Pseudocalanus minutus*. Since *P. minutus* is about 10 times the body weight of the Paracalanidae in Kaneohe Bay, the rates are not directly comparable. The study of Petipa, Pavlova, and Mironov (1970) measured the consumption rate:biomass ratio during summer for a group of small species including *Oithona minuta*, *Paracalanus parvus*, and *Acartia clausi* (which is about twice the size of the Paracalanidae in Kaneohe Bay). The consumption rate of the group ranged from 45 percent of the body weight for late copepodids to 140 percent for nauplii. The consumption rate, if converted to growth rates with a gross growth efficiency ratio of $\frac{1}{4}$ to $\frac{1}{3}$ as previously described, indicate a range of production rate:biomass ratios of 11 to 47 percent per day. These ratios are $\frac{1}{4}$ to $\frac{1}{2}$ times the ratios found for the Paracalanidae of a similar size and stage during the present study.

Lastly, there have been two studies of neritic microcopepods which, similar to the present one, have measured rates of growth or yield. First, Heinle (1966) determined the rate of growth and population stage composition for *Acartia tonsa* during summer in a Chesapeake Bay estuary. The population yield rate:biomass ratio averaged 50 percent per day, which is about $\frac{2}{3}$ times the similar ratio for Paracalanidae in Kaneohe Bay. Second, Mullin and Evans (1974) grew copepod populations in a large tank and continually harvested the population "yield" with a plankton net, the "predator". The daily population yield:biomass ratios were 22 percent for *Paracalanus parvus* and 10 percent for *Acartia tonsa*. The ratio for *Paracalanus parvus* is about $\frac{1}{4}$ times the ratio for the Paracalanidae population in Kaneohe Bay. One reason why the ratio of Mullin and Evans (1974) is comparatively low may be that the food concentration in their tank was about $\frac{1}{3}$ times the average environmental concentration.

The calculated 78-percent population production rate:biomass ratio for Paracalanidae is probably high for the natural field population during summer in southern Kaneohe Bay. The high ratio is probably related to the high temperature and abundant food concentration present when the Paracalanidae development rate was measured. The average summer ratio may be about $\frac{1}{2}$ to $\frac{2}{3}$ times the calculated ratio, or in the range of values that were obtained by Petipa, Pavlova, and Mironov (1970) and Heinle (1966) with microcopepods during spring–summer. The maximum ratio may be about twice the calculated 78 percent ratio, as indicated by the study of Szyper (1972).

To calculate the secondary production of all the microcopepods in southern Kaneohe Bay, we estimated the production rate:biomass ratios of the *Oithona* species from the ratio of Paracalanidae. We used the exponential rates of net increase of copepodids during periods of rapid population increase, as stated earlier, to estimate the species' gross rates of population production. The relationship of the exponential rates indicates that the rates of population production per unit biomass were highest for Paracalanidae and were 38 percent lower for *O. nana* and *O. simplex*.

The population biomass for Paracalanidae during August 1968 averaged about 20 mg dry wt/m^3 for the upper 11 m of the water column. The population biomasses of Paracalanidae,

O. simplex and *O. nana* in southern Kaneohe Bay in August 1968 (Table 2) were estimated to be 64, 18, and 18 percent, respectively, of the total microcopepod biomass. Since the population biomass of Paracalanidae averaged 20 mg dry wt/m^3, the population biomasses of *O. simplex* and *O. nana* would have equalled about 6 mg dry wt/m^3 for each species. The relationship of the species' production rate:biomass ratios to the ratio of 78 percent per day for Paracalanidae indicates that the population production rate of Paracalanidae, *O. simplex* and *O. nana* during summer 1968 equalled about 16, 3, and 3 mg dry wt/m^3/day, respectively. The secondary production rate of all three species would have equalled about 22 mg dry wt/m^3/day or, with the dry wt:nitrogen wt ratio of 12.0:1.0, about 1.8 mg nitrogen/m^3/day. With a gross growth efficiency ratio of $\frac{1}{4}$ to $\frac{1}{3}$ as described previously, the total microcopepod consumption and excretion rates should have equalled about 1.2 and .5 mg nitrogen/m^3/day, respectively, during summer 1968 in southern Kaneohe Bay. The entire mirocopepod rates may be attributed to the herbivorous trophic level because of the species' characteristic foods. The mainly carnivorous zooplankton from 333-μm net samples in southern Kaneohe Bay excreted comparable amounts of nitrogen (.7 mg/m^3/day) during the early spring of 1974 (Szyper et al. 1976).

The difference in the production rate:biomass (P:B) ratios of subtropical neritic and oceanic copepods may provide an insight on the nature of the southern Kaneohe Bay planktonic community. The P:B ratios that have been calculated for subtropical oceanic copepods (Petipa, Pavlova, and Sorokin 1971; Newbury, in press) are generally lower than the reviewed ratios for subtropical coastal and neritic microcopepods. One reason for the difference in ratios may be due to the relative instability or unpredictability of the populations and their food supply in neritic communities, as indicated by Figure 1 for southern Kaneohe Bay. Unpredictability of a community's food web usually favors opportunistic, *r*-selected species with high, potential P:B ratios (Odum 1969, MacArthur and Wilson 1967). The association of unpredictability and species with high P:B ratios implies that the present southern Kaneohe Bay planktonic community persists because of the irregular fluctuations in concentrations of nutrients and particulate matter (see Caperon, Harvey, and Steinhilper 1976: figure 2). The association also implies that the southern Kaneohe Bay planktonic community might undergo a great change in composition if sewage were used to stabilize the fluctuations of nutrients that derive from the periodic runoff from the surrounding, developed lands.

SUMMARY

1. Analyses of the fluctuations in abundance of the microcopepods showed that during spring the Paracalanidae population was the first to increase in abundance in southern Kaneohe Bay. During several periods of population increase in abundance, the exponential rates of increase of copepodids averaged 38 percent lower for both *Oithona simplex* and *O. nana* than for Paracalanidae.
2. The population biomass of Paracalanidae was about 20 mg dry wt/m^3 during August 1968, the period for which production was calculated. The population biomass of Paracalanidae was about 3.5 times greater than for either *Oithona* species during both the relatively stable period of August 1968 and for the whole year.
3. The life span of Paracalanidae was about 1 week in both the laboratory and *in situ* containers. Because of the 27° to 30° C temperature and abundant food in the containers, the development rate was probably more rapid than that of the natural population during summer in the Bay.
4. The Paracalanidae population production rate:biomass ratio during summer was calculated to be 78 percent per day. This ratio is higher than the values for similar-sized neritic microcopepods in other environments and may be one-half of the maximum ratio for the Paracalanidae in southern Kaneohe Bay.
5. For all of the microcopepod species, secondary production during summer in southern Kaneohe Bay was estimated to be 1.8 mg nitrogen/m^3/day.

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